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Impact of short-term high temperature on adult survival and fitness of the oriental fruit moth, *Grapholita molesta* (Lepidoptera: Tortricidae)

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Abstract:【Aim】The oriental fruit moth, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae), is a worldwide fruit pest, causing serious loss to fruit productivity. Our study aims to explore the thermal tolerance and adaptability of *G. molesta* adults after exposure to short-term high temperature.【Methods】The survival rate of *G. molesta* adults exposed to various temperatures (36, 38, 40, 42, 44 and 46℃) for different time durations (0.5, 1, 2, 4 and 8 h), and the effects of short-term high temperature exposure (heat hardening at 38 or 40℃ for 1 h) on their thermal tolerance, longevity, fecundity, and egg hatchability were investigated.【Results】The results showed that the survival rate of *G. molesta* adults was reduced with the increase of exposure duration to high temperature. The survival rate of *G. molesta* adults at 42℃ was significantly improved after adults were subjected to heat hardening at 38℃ or 42℃ for 1 h ($P < 0.05$). After treatment at 41℃ for 1 h, *G. molesta* adults were heat shocked, with longer life span and less fecundity. The further study confirmed that the male adults were greatly affected by high temperature, resulting in the reduction of eggs laid by female adults paired. Nevertheless, there was no remarkable difference in egg hatchability in different treatments though their parents underwent thermal stress.【Conclusion】These results suggest that high temperature exceeding 41℃ for 1 h causes negative effects to *G. molesta* adults, but *G. molesta* adults have a relatively high thermal tolerance and the potential to adapt to high temperatures.

Key words: *Grapholita molesta*; temperature; fecundity; longevity; survival rate; thermal stress

1 INTRODUCTION

Insects are small-bodied ectotherms, whose body temperatures are determined to a large extent by environmental temperature (Denlinger and Yocum, 1998; Angilletta *et al*., 2002). Therefore, they are easily affected by natural temperature fluctuating, and temperature is considered as the major abiotic factor which has a profound effect on distribution, abundance, behavior, fitness and the life history of insects in general (Denlinger and Yocum, 1998; Hoffmann *et al*., 2003). Insects are typically exposed to constant temperatures for an entire generation or across multiple generations to estimate the effects of heat stress on them in most previous studies (Denlinger and Yocum, 1998; Mironidis and Savopulou-Soultani 2010; Guo *et al*., 2012). The unsuitable temperature can lead to diverse detrimental effects on insects such as developmental delay (Luo *et al*., 2005), physical deformity (Ma and Chen, 1993; Williams *et al*., 2003), impaired fertility (Schnebel and Grossfield, 1984; Mahroof *et al*., 2005), diapause (Butler *et al*., 1985; Nibouche *et al*., 1998; Ishikawa *et al*., 2000; Teixeira and Polavarapu, 2005) and even immediate death (Dean *et al*., 1974; Pelletier *et al*., 1998; Wright *et al*., 2001; Boina and Subramanyam, 2004; Wang *et al*., 2004). However, high temperature under field conditions daily could not be constant and might only last for a few hours. The influence of short-term high temperature on insects has received more attention recently (Zizzari and Ellers, 2011; Chang *et al*., 2012; Piyaphongkul *et al*., 2012; Zhang *et al*., 2013), because the intensity and frequency of extreme high temperatures are expected to increase in the future under global warming (Meehl and Tebaldi, 2004; Rahmstorf and Coumou, 2011).

The oriental fruit moth, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae), is one of the most important insect pests damaging stone and pome

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fruits mainly belonging to the Rosaceae family (Chapman and Lienk, 1971; Rothschild and Vickers, 1991). This pest species can be found in various stages during the entire growing season, and its larvae can bore into the fruit or shoot of its host, causing serious economic loss to fruit productivity (Hughes and Dorn, 2002; Myers *et al.*, 2006). Piskorski *et al.* (2011) found that *G. molesta* had the ability of tolerance to high-level juglone, a kind of toxic substance produced by non-host of *G. molesta*, thus had the potential to expand its host range beyond the current Rosaceae fruit trees. Therefore, it is still a kind of very dangerous pest.

In laboratory rearing studies, the optimal temperature range for survival, development and reproduction of *G. molesta* is 23 - 29℃ (Du *et al.*, 2009). However, the temperature is normally above 30℃ from June to September in northern China, which is also the outbreak period of *G. molesta* adults, and the highest temperature during one day can exceed 39℃ (Cui *et al.*, 2008). At present, due to the ongoing global warming, the frequency and intensity of high temperatures are predicted to increase substantially (Easterling *et al.*, 2000; Diffenbaugh *et al.*, 2005), which increases the chance of exposure to short-term high temperature in an accidental hot day for *G. molesta*. How much is the thermal threshold of *G. molesta*? How will the short-term high temperature impact this species? Understanding these two questions has important implications for monitoring population dynamics and dispersal of this insect pest in the future, and for developing sustainable integrated strategies of management. Survival of the eggs and larvae of *G. molesta* after short-term exposure to high temperature was investigated by Yokoyama and Miller (1987). Ltime_{50} (time required for 50% mortality) and the temperature and exposure duration required for 100% mortality were reported, but the information about adults of this insect pest remains unclear. Adult stage is one of developmental stages exposing to natural environments, which contributes directly to changes in population size of the next generation through reproduction. In this study, we determined the range of time-temperature combinations which may be lethal or sub-lethal at short time scales to give insight into thermal tolerance of this species and investigated the effects of short-term high temperature on their longevity and fecundity.

2 MATERIALS AND METHODS

2.1 Insects

G. molesta were originally collected from peach shoots in Yangling, shaanxi, China in 2010. Larvae were reared with artificial diets described by Du *et al.* (2010). The artificial climate chamber (Shanghai Yiheng Instruments Co., Ltd) used to rear *G. molesta* was maintained at 26 ± 1℃, with a relative humidity of 75% ± 10% and a photoperiod of 15L: 9D. The 24 - 36 h-old adults after eclosion were chosen in this study.

2.2 Effects of high temperature on survival of adults

Adults were collected in thin-walled test tubes (110 mm in length × 13 mm in diameter, 8 - 10 individuals per tube) blocked with cotton balls. All tubes were submersed into a water bath (Huangshi Hengfeng Medical Instrument Co., Ltd, the increase rate of temperature was approximately 1℃ per min) for heat treatment at the target temperatures (36, 38, 40, 42, 44 and 46℃) for different time durations (0.5, 1, 2, 4 and 8 h). At the end of exposure, insects were transferred to 26℃ for recovery, and the number of dead individuals was recorded 24 h later (Some individuals were still alive at the end of heat treatment, but they would die in the following hours). Adults were considered dead if they had no response to gentle prodding by a small Chinese writing brush. *G. molesta* adults undergoing the time duration of 8 h at 26℃ were used as the control. Neither water nor food was supplied to adults in the whole heat treatment process. Each treatment consisted of 20 adults (sex ratio = 1∶1), and was replicated five times.

2.3 Effects of heat hardening on survival

Thirty-two adults (sex ratio = 1∶1) in each treatment were pre-treated at target temperatures including 26, 38 and 40℃ for 1 h, respectively, then transferred to 26℃ for recovery. Twenty-four hours later, they were heated at 42℃ for 2 h. The number of dead individuals was recorded 24 h later to calculate the survival rate. There was no water or food supply to adults in the whole heat treatment process. Each treatment was replicated thrice.

2.4 Effects of high temperature on longevity and reproduction

Thirty-two adults (sex ratio = 1∶1) were exposed at the target temperature including 26, 29, 32, 35, 38, 41 and 44℃, respectively for 1 h. Subsequently, adults in the same temperature treatment were transferred to a 500 mL glass beaker respectively, with a wet cotton ball (changed every 3 days) in it for water supply, and a transparent plastic sealing film (changed daily) blocked on the beaker mouth. All beakers were placed into a climate chamber with the same condition of *G. molesta* maintained. The whole beaker was covered by a black cloth except the side of plastic sealing film, which would help to obtain the great majority of eggs on the film. Number of eggs laid and dead adults were counted daily. Sealing films with eggs were kept in chamber to record the hatchability 7 days later (according to the previous trial, eggs of *G. molesta* should hatch within 4 d at 26℃). Each treatment was replicated four times.

2.5 Effects of high temperature on fecundity

In group A, 16 female adults were heated at 41℃ for 1 h, and 16 male adults were heated at 26℃. In group B, there were 16 male adults heated at 41℃ and 16 female adults heated at 26℃. In group C, 32 adults (sex ratio = 1∶1) were heated at 41℃. Thirty-two adults (sex ratio = 1∶1) heated at 26℃ were made as the control (CK). After heat treatment, adults in same group were paired in a 500 mL glass beaker and maintained at 26℃ for reproduction. The methods of heat and observation were the same as that used above. Number of eggs laid was recorded daily. Each treatment was replicated thrice.

2.6 Statistical analysis

The time required to achieve 50% and 90% mortality (Ltime$_{50}$ and Ltime$_{90}$) were estimated by Probit analysis using SPSS 16.0 software (SPSS Inc.). Statistically homogenous groups were identified using overlap in 95% confidence limits (Finney 1952; Chidawanyika and Terblanche, 2011).

The significant differences between treatments were analyzed by one-way analysis of variance (ANVOA) followed by the Student-Newman-Keuls Test (SNK) for multiple comparisons. The data were analyzed using SPSS 16.0 software. The significance level used for all statistical tests was $P = 0.05$.

3 RESULTS

3.1 Survival rate and lethal time of *Grapholita molesta* adults after exposure to different high temperatures for different time durations

The survival rate of *G. molesta* adults declined with the increase in exposure duration and exposure temperature (Fig. 1). For example, the survival rate was near to 90% (88.00% ± 3.00%) when the adults were exposed to 36℃ for 8 h, while near to zero when the adults were exposed to 42℃ for 4 h. About half of adults could survive when exposed to 44℃ for 0.5 h, but no adults survived when the exposure time exceeded 1 h. At 46℃, no adult could survive when the exposure time was longer than 1 h. No adult in the control group (26℃ for 8 h) died.

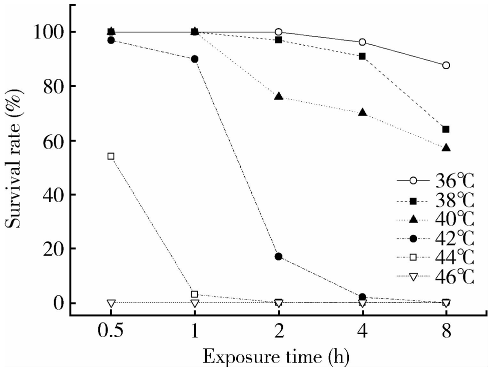

Fig. 1 Survival rate of *Grapholita molesta* adults after exposure to different high temperatures for different time durations

Ltime$_{50}$ and Ltime$_{90}$ for *G. molesta* adults at various high temperatures are shown in Table 1. When the temperature was lower than 40℃, the Ltime$_{50}$ and Ltime$_{90}$ values were longer than 8 h. There was significant difference among the Ltime$_{50}$ values at the four temperatures from 40 to 46℃, but the Ltime$_{90}$ values at 44 and 46℃ did not differ significantly.

3.2 Survival rate of *Grapholita molesta* adults after heat hardening

After the short-term high temperature hardening (38 and 40℃ for 1 h), the survival rate of *G. molesta* adults increased significantly compared with the control (26℃) (19.86% ± 6.74%; $F_{2,6} = 9.79$, $P = 0.013$) (Fig. 2). However, the survival rate did not vary significantly between 38 (50.50% ± 5.28%) and 40℃ (41.21% ± 1.54%).

Table 1 Lethal time for *Grapholita molesta* adults at various high temperatures

Temperature (℃)	*d.f.*	Ltime$_{50}$ (95% CI) (min)	Ltime$_{90}$ (95% CI) (min)	χ^2	*P*-value
40	3	> 480	> 480	–	–
42	3	88.04 (67.58 – 115.13)	153.64 (117.04 – 275.40)	16.901	0.02
44	3	28.56 (26.22 – 31.10)	52.30 (46.47 – 61.06)	5.665	0.226
46	3	15.50 (8.02 – 20.14)	29.56 (23.43 – 58.35)	14.027	0.015

d.f.: Degree of freedom for chi-square test; χ^2: Calculated value of chi-square; *P*-value: Probability of a greater chi-square. Number of tested individuals in each temperature treatment is 100. Ltime values are considered significantly different when 95% confidence intervals fail to overlap.

3.3 Longevity and reproduction of *Grapholita molesta* adults at different temperatures

After exposure to 41℃, all adults were heat shocked. They dropped down on the bottom of test tubes, only with their legs and antennae moving slightly, but they would recover in the following 2

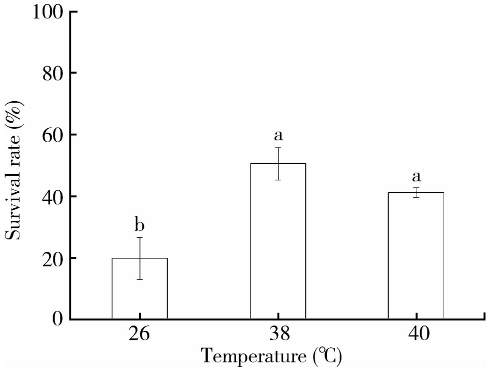

Fig. 2　Survival rate of *Grapholita molesta* adults after heat hardening

Adults were heated at different temperatures 26, 38 and 40℃, respectively, for 1 h and allowed to recovery at 26℃ for 24 h. Subsequently, adults were heated at 42℃ for 2 h. Different letters above bars indicate significant difference by ANOVA analysis (SNK: $P < 0.05$).

hours when put back to 26℃. After exposure to 44℃, all adults were dead.

The longevity of adults increased with the exposure temperature rising ($F_{11,511} = 7.28$, $P < 0.001$), except at 38℃, which did not differ from that at 26℃ (Fig. 3). Male adults at 41℃ (11.46 ± 0.68 d) and 35℃ (12.09 ± 0.57 d) lived longer than those at 26℃ (9.12 ± 0.33 d), while female adults at 41℃ (12.48 ± 0.60 d) lived longer than those at 26℃ (9.13 ± 0.39 d). Nevertheless, at the same temperature, there was no significant difference in the longevity between female and male.

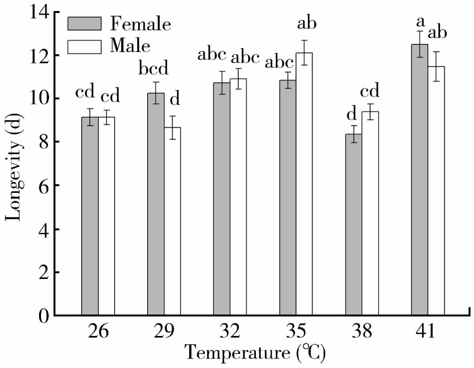

Fig. 3　Longevity of *Grapholita molesta* adults at different temperatures

Adults were heated at different temperatures for 1 h, and then maintained at 26℃. Different letters above bars indicate significant difference by ANOVA analysis (SNK: $P < 0.05$).

The mean number of eggs laid per female remarkably decreased when adults were heated at 41℃ for 1 h ($F_{5,18} = 3.64$, $P = 0.019$) (Fig. 4). It changed from 53.13 ± 4.39 at 26℃ to 27.17 ± 3.81 at 41℃. There was no significant difference in the mean number of eggs laid per female when the adults were exposed to the other temperatures. Also, there was no difference in hatching rate of eggs at various temperatures ($F_{5,12} = 0.25$, $P = 0.93$) (Fig. 5). The egg hatchability in all treatments was higher than 98%.

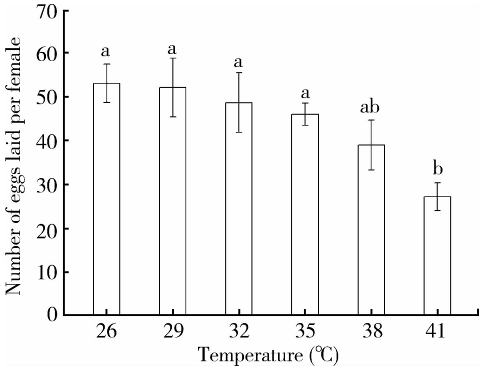

Fig. 4　Number of eggs laid per female of *Grapholita molesta* at different temperatures

Adults were heated at various temperatures for 1 h, then paired and maintained at 26℃ for reproduction. Different letters above bars indicate significant difference by ANOVA analysis (SNK: $P < 0.05$).

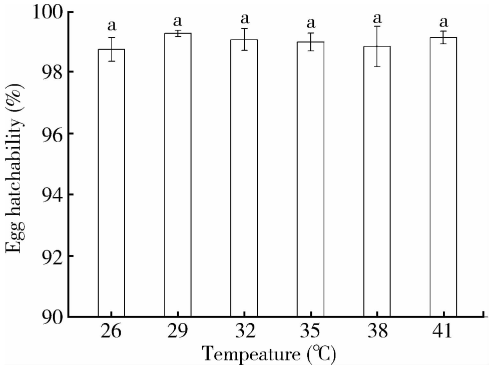

Fig. 5　The hatchability of eggs produced by *Grapholita molesta* female adults at different temperatures

Adults were heated at various temperatures for 1 h, then paired and maintained at 26℃ for reproduction. The statistical significance between treatments was analyzed by ANOVA analysis (SNK: $P < 0.05$).

3.4　Impairment of fecundity of *Grapholita molesta* adults at different temperatures

The number of eggs laid per female remarkably decreased when male adults were subjected to high temperature treatment ($F_{3,8} = 21.485$, $P = 0.001$), namely in group B (30.41 ± 1.52) and group C (28.73 ± 2.57). The number of eggs laid per female in group A (45.61 ± 3.07) and CK (53.55 ± 2.92) did not differ significantly (Fig. 6).

4　DISCUSSION

In ectothermic organisms, survival and reproductive success are vitally affected by temperature. This study considered the impact of short-term high temperature on the performance of adults of *G. molesta*, one of the most destructive and

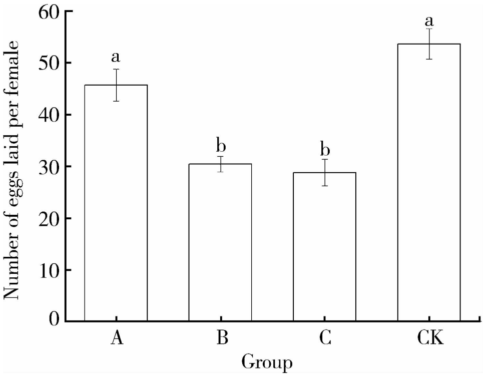

Fig. 6 Number of eggs laid per female of *Grapholita molesta* in different groups

A: Female adults were heated at 41℃ for 1 h, and males were at 26℃; B: Male adults were heated at 41℃ for 1 h, and females were at 26℃; C: Female and male adults were heated at 41℃ for 1 h; CK: Female and male adults were heated at 26℃ for 1 h. After heat treatment, adults in the same group were paired and maintained at 26℃ for reproduction. Different letters above bars indicate significantly different means by ANOVA analysis (SNK: $P < 0.05$).

economically important fruit pests. Temperatures lethal to insects are a function of both the magnitude of the temperature variation and the duration of exposure (Chown and Nicholson, 2004; Angilletta, 2009), the higher the temperature the shorter the exposure needed to kill the insect (Denlinger and Yocum, 1998), so the present study attempted to determine the survival rate of *G. molesta* adults under varying high temperatures for different short durations. Our results showed that 90% individuals could survive more than 4 h at 38℃ and 50% individuals could survive more than 8 h at 40℃, which indicates that *G. molesta* adults have a relative high thermal tolerance. Short-term heat hardening at non-lethal high temperature remarkably improved the survival rate of adults when they encountered lethal temperature again. These suggest that heat hardening can induce the phenotypic plasticity of thermal tolerance of *G. molesta*. Induction of such plastic responses can be achieved after pre-exposure to sub-lethal temperatures or perhaps also in anticipation of extremes (Chown and Terblanche, 2007), enabling insects to survive what would otherwise be lethal conditions. Our data suggest that the high thermal tolerance and the plastic response to high temperature are the reasons that *G. molesta* adults can survive in the hot summer days.

Earlier studies have reported the longevity of some insects would increase after undergoing a short period of heat stress (Maynard, 1958; Olsen *et al.*, 2006; Scannapieco *et al.*, 2007; Zhang *et al.*, 2012). In the present study, the longevity of adults has the tendency to increase in comparison to the control. Insects can survive from thermal stress by the synthesis of stress proteins and other key metabolites (Denlinger and Yocum, 1998; Hendrix and Salvucci, 1998; Feder and Hofmann, 1999; Huang *et al.*, 2007). It is thought that the increased longevity may benefit from the synthesis of these substances, such as antioxidant enzymes or heat shock proteins (Orr and Sohal, 2003; Morrow *et al.*, 2004), but this need extra energy costs, and the effect between costs and benefits is complex when insects go through a harmful temperature (Denlinger and Yocum, 1998; Hoffmann *et al.*, 2003; Huang *et al.*, 2007). The complex tradeoff effect was also found in our results, which showed that the longevity of adults increased with the temperature rising except at 38℃.

Our results suggest that the exposure to 41℃ produces negative effects on adults. For example, they needed a short period of time for recovery from heat shock status, and the number of eggs laid decreased dramatically. Heat shock exposure has been shown to strongly affect the reproductive fitness of various insect species (Krebs and Loeschcke, 1994; Mironidis and Savopoulou-Soultani, 2010; Roux *et al.*, 2010; Piyaphongkul *et al.*, 2012), but they could not determine which sex or both were affected. In our following studies, the results confirmed that male adults were greatly affected by high temperature. The impairment of ability to locate females can be excluded, because male adults can find females easily in the space of a 500 mL beaker in such density. In some insects, it has been found that heat shock can reduce male fertility due to direct injury to the testes and sperm (Chihrane and Lauge, 1994, 1997; Krebs and Loeschcke, 1994; Rinehart *et al.*, 2000; David *et al.*, 2005). Also, there were reports about high temperature could disrupt the normal reproductive function of females or both sex (Rinehart *et al.*, 2000; Cui *et al.*, 2008), but in our present study, no evidence proved that the fecundity of female adults was influenced significantly by high temperature. This indicates that, to some extent, female adult is more thermal tolerant than male.

In some insects, the hatchability of eggs laid by stressed female was significantly reduced, which may be related to the reduction of synthesis of yolk nutrition and chorion component (Sørensen *et al.* 2005). However, our results showed that high temperature has little maternal effect on the hatchability of laid eggs. This phenomenon is in agreement with the study of Huang *et al.* (2007) on *Liriomyza huidobrensis*. Of course, the subsequent effect of high temperature on larvae hatched still needs further research.

Finally, short-term high temperature may produce negative effects on the male reproduction system of *G. molesta*. Nevertheless, eggs are produced by female adults which can mate several times in the whole life (Rothschild and Vickers, 1991), and no significant maternal effects were observed on their offsprings. Thus, short-term high temperature may have little effect on the next generation. *G. molesta* adults have a strong thermal tolerance and may have the potential to adapt to high temperature. There is little influence of short-term high temperature on *G. molesta* population in hot day; hence, it is still a very dangerous insect pest in the future.

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短期高温对梨小食心虫成虫存活率和适应性的影响

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摘要：【目的】梨小食心虫 *Grapholita molesta*(Busck)(鳞翅目:卷蛾科)是一种世界性的害虫,能使蔷薇科的果树严重减产。本研究旨在评估此害虫的耐热性及适应性。【方法】将梨小食心虫成虫暴露在不同温度(36, 38, 40, 42, 44 和46℃)和不同暴露时间(0.5, 1, 2, 4 和8 h)下,测定其存活率以及短期高温(38 或40℃热驯化1 h)对其热耐受力、寿命、生殖力及卵孵化率的影响。【结果】随着高温暴露时间的延长,梨小食心虫成虫存活率下降。在38 或40℃热驯化1 h后,能显著提高梨小食心虫成虫在42℃下2 h的存活率($P < 0.05$)。在41℃处理1 h,梨小食心虫出现热休克现象,其寿命显著延长,但产卵量显著下降。进一步的试验证明雄虫受高温影响较大,导致与其配对后的雌虫产卵量降低。然而,不论亲代受到怎样的热刺激,其后代的孵化率均不受影响。【结论】结果说明,超过41℃,1 h的高温能对梨小食心虫带来负面影响,但梨小食心虫成虫有适应高温的潜力。

关键词：梨小食心虫；温度；生殖力；寿命；存活率；热胁迫

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